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Genetic parameters for meat quality traits of Australian lamb meat

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Abstract

Genetic parameters were estimated for a range of meat quality traits recorded on Australian lamb meat. Data were collected from Merino and crossbred progeny of Merino, terminal and maternal meat breed sires of the Information Nucleus programme. Lambs born between 2007 and 2010 ($n=8968$) were slaughtered, these being the progeny of 372 sires and 5309 dams. Meat quality traits were found generally to be of moderate heritability (estimates between 0.15 and 0.30 for measures of meat tenderness, meat colour, polyunsaturated fat content, mineral content and muscle oxidative capacity), with notable exceptions of intramuscular fat (0.48), ultimate pH (0.08) and fresh meat colour a^* (0.08) and b^* (0.10) values. Genetic correlations between hot carcass weight and the meat quality traits were low. The genetic correlation between intramuscular fat and shear force was high (-0.62). Several measures of meat quality (fresh meat redness, retail meat redness, retail oxy/met value and iron content) appear to have potential for inclusion in meat sheep breeding objectives.

Keywords: intramuscular fat; lamb; tenderness; meat colour; minerals content; fatty acid composition.

1. Introduction

Improvement of the quality of Australian lamb meat, particularly eating quality and nutritional value, will enhance the industry's capacity to meet increasing consumer expectations for lamb products (Pethick, Ball, Banks & Hocquette, 2011). Over the last two decades, the Australian sheep meat industry has delivered large increases in lamb production and profitability, with genetic improvement in growth, leanness and muscling making a substantial contribution to these gains (Fogarty, 2009). There is evidence that continued selection for leanness (higher lean meat yield) may adversely affect aspects of eating quality and intramuscular fat content (Hopkins, Hegarty & Farrell, 2005; Karamichou, Richardson, Nute, McLean & Bishop, 2006b). Hence, Pethick et al. (2011) asserted that genetic improvement programmes will have an important role in contributing to the enhancement of

meat quality of lamb, although it will be a complex task to determine the important component traits for eating quality and nutritional value that should be measured on an on-going and cost-effective basis.

Genetic variation exists for some meat quality traits, as reviewed by Hopkins, Fogarty & Mortimer (2011). While estimates of heritability for some traits have been reported, there are few published estimates of genetic and phenotypic correlations among meat quality traits or with other production traits. Information on heritabilities and genetic correlations among meat quality traits is needed to identify their importance in breeding programmes that efficiently improve lamb meat quality and productivity. Using data from progeny of the Information Nucleus Flock programme of the Co-operative Research Centre for Sheep Industry Innovation (Fogarty, Banks, van der Werf, Ball, & Gibson, 2007; van der Werf, Kinghorn, & Banks, 2010), this study aims to estimate heritability for a range of meat quality traits as well as the genetic and phenotypic correlations among the traits. The traits include those relevant to eating quality and tenderness, fresh and retail meat colour, nutritional value and hot carcass weight. The environmental effects influencing these meat quality traits have been identified and were reported recently by Jacob, D'Antuono, Gilmour, & Warner (2013), Kelman, Pannier, Pethick, & Gardner (2013), Pannier, Pethick, Boyce et al. (2013a), Pannier, Pethick, Geesink et al. (2013b) and Ponnampalam et al. (2013). Using a sub-set of the data, an earlier study by Mortimer et al. (2010) reported preliminary genetic parameter estimates for some meat quality traits, as well as live animal and carcass traits, and identified intramuscular fat and shear force as potential traits for inclusion in sheep breeding objectives. The present paper provides a more extensive report on the genetic parameters for a wider selection of meat quality traits than previous reports.

2. Materials and Methods

2.1. Animals

Data were collected over a 5 year period (2007 to 2012) from the crossbred and Merino progeny of the Information Nucleus breeding programme at eight research sites and a commercial farm around Australia. The design of the Information Nucleus has been described fully by van der Werf et al. (2010), including the procedure used to select the sires for AI mating with the flocks' base ewes. Sires were selected from a range of breeds used in the Australian sheep industry (Merino, maternal and terminal meat breeds). The base ewes, depending on the research farm location, were drawn from pedigreed and/or commercial flock sources and usually consisted of approximately 80% Merino ewes and 20% Border Leicester x Merino ewes. The results presented herein were generated from records from 8968 slaughtered lambs, born between 2007 and 2010. These lambs were the progeny of 372 sires and 5309 dams and were born in 6915 litters. The average number of lambs slaughtered was 1.7 per dam. Data for intramuscular fat, shear force (after 5 days of ageing), mineral traits, fatty acids and myoglobin content were available on lambs born 2007-2009 and on isocitrate dehydrogenase activity for lambs born 2007-2008. The retail color traits were recorded only on progeny born 2007-2010 at the Cowra, Trangie, Hamilton, Rutherglen and Katanning sites.

Once weaned, the lambs at each site were managed to achieve target carcass weights of 21-22 kg, with target growth rates of 200 g/day for crossbred lambs and 150 g/day for Merino lambs prior to slaughter. The nutritional history of the lambs at each site is given by Ponnampalam et al. (2013). The lambs usually grazed the extensive pastures available at the sites, but were supplemented with grain, hay or feedlot pellets when the pasture supply was restricted. Each year, a fasted weight (2 h off feed and water) recorded one week prior to slaughter was used to allocate the lambs to a slaughter group, balanced for weight within sex, sire and production types used in Australian sheep industry (Merino, Border Leicester X Merino, terminal meat breed X Merino and terminal meat breed X Border Leicester-Merino). All lambs were slaughtered at commercial abattoirs. The average age at slaughter in days (standard deviation) was: 258 (64.3) for 2007-born lambs across 30 slaughter groups; 281 (86.6) for 2008-born lambs across 29 groups; 256 (59.5) for 2009-born lambs across 28 slaughter groups; and 260 (65.0) for 2010-born lambs across 30 slaughter groups.

2.2. Lamb slaughter and measures

The post-slaughter sampling protocol for the carcass and meat quality traits is described by Pearce (2009). Briefly, all carcasses were subjected to medium voltage electrical stimulation and trimmed according to AUS-MEAT specifications (Anonymous 1992). At slaughter, hot carcass weight (HCWT) was recorded. A sample (1 g) taken from the *M. longissimus thoracis et lumborum* (LL), was frozen in liquid nitrogen within 2 h of death and subsequently assayed for isocitrate dehydrogenase (ICDH; EC 1.1.1.42) according to a procedure described by Gardner, Pethick, Greenwood, & Hegarty (2006). Carcasses were chilled overnight (3-4°C) and then were cut between the 12th and 13th ribs to expose the surface of the LL. At 24 h post-mortem, the lumbar portion of the LL muscle was excised from the carcass.

2.3. Meat quality measurements

The cut surface of the LL at the 12th rib was exposed to the air at ambient temperature for 30-40 min and the meat colour measured as described by Warner et al. (2010), using Minolta Chroma meters (Models CR-300 and CR-400) set on the L^* , a^* , b^* system (where L^* (cfL^*) measures relative lightness, a^* ($cf a^*$) relative redness and b^* ($cf b^*$) relative yellowness). Three replicate measurements were taken at different positions and an average value used for analysis. The pH of the LL was measured at approximately 24 h (pH_{24LL}) after slaughter using a number of different pH meters linked to pH electrodes calibrated at chiller temperatures (3-4°C) (Pearce et al., 2010). After removal of subcutaneous fat and epimysium from the excised LL muscle, two 40 g samples of diced muscle were collected, frozen and stored as described by Pannier et al. (2010). Iron and zinc contents were measured on one sample as described by Pannier et al. (2010), while a range of fatty acids was measured on the other sample, including the long chain omega-3 fatty acids eicosapentaenoic acid (EPA, 20:5n-3), docosapentaenoic acid (DPA, 22:5n-3) and docosahexaenoic acid (DHA, 22:6n-3).

and omega-6 fatty acids linoleic acid (LA, 18:2n-6) and arachidonic acid (ARA, 20:4n-6) as described by Ponnampalam et al. (2010). Totals for the fatty acids were calculated for each sample of: EPA and DHA (EPA+DHA); EPA, DPA and DHA (EPA+DPA+DHA); and LA and ARA (LA+ARA).

Myoglobin content (Myo) was measured on a sample (1 g) taken from the loin using methods described by Trout (1991). A sample (50 g) was also taken for analysis of intramuscular fat (IMF) and then frozen before storage (Pannier et al., 2013b). Percentage of IMF was determined using a near infrared procedure (NIR) in a Technicon Infralyser 450, as described by Perry, Shorthose, Ferguson & Thompson (2001). Meat colour stability under simulated retail display was measured on a 3 cm slice from the cranial end of the LL which had been vacuum packed and aged for 5 days. Further details are provided by Jacob et al. (2013). Data analysed herein (prefixed ret) were recorded after 2 days of simulated retail display. These data included L^* (ret L^*), a^* (ret a^*), b^* (ret b^*) and oxymyoglobin/metmyoglobin value (retOxy/Met or oxy/met value). Psychometric hue angle (reth) and psychometric chroma (retC*) were calculated as $\text{psychometric hue} = \tan^{-1} (b^*/a^*)$ and $\text{psychometric chroma} = (a^{*2} + b^{*2})^{0.5}$ (Hunt et al., 1991). A section of the LL (65 g) was aged for 5 days at 3-4°C, and stored frozen. For shear force testing (SF5), these samples then were cooked from frozen for 35 min in plastic bags at 71°C in a water bath and tested using a Lloyd texture analyser (Model LRX, Lloyd Instruments, Hampshire, UK) with a Warner-Bratzler type shear blade fitted as described by Hopkins, Toohey, Warner, Kerr & van de Ven (2010).

2.4. Statistical analyses

All analyses of the data were conducted using the software ASReml (Gilmour, Gogel, Cullis, Welham & Thompson, 2009) and restricted maximum likelihood procedures. Initially, a mixed linear model was used to identify those fixed effects influencing the traits, which included the fixed effects of site, year of birth (4, 3 or 2 levels), slaughter group, sire breed

(19 levels: Border Leicester, Bond, Booroola Merino, Corriedale, Coopworth, Dohne Merino, East Friesian, Hampshire Down, Ile de France, Merino (ultrafine/superfine wool type), Merino (fine/medium wool type), Merino (medium/strong wool type), Poll Dorset, Southdown, Prime South African Meat Merino, Suffolk, Texel, White Suffolk or Dorper), dam breed (2 levels: Merino or Merino x Border Leicester), sex (2 levels: male castrate or female), type of birth and rearing (6 levels: 11, 21, 22, 31, 32 or 33 for lambs born and reared respectively) and dam age (7 levels: 1 to greater than or equal to 7 years of age). Age of the lamb was fitted as a linear covariate. The data for the fatty acids were log-transformed for analyses. Significant ($P < 0.05$) two-way interactions were included in the final model. Univariate mixed model analyses were used to obtain estimates of variance components for each trait. All models included a random animal effect, representing the additive genetic variance. A fixed genetic group effect also was fitted to account for the base animals being from different breeds and strains and was fitted according to the 'phantom parent' approach as described by Westell, Quaas & van Vleck (1988). Random effects of sire x site interaction, dam (representing a maternal effect comprising both maternal genetic and maternal environmental effects) and dam x year interaction (representing environmental variation between litters) were then added to the model to assess the importance of these effects in explaining variation in each trait. If its inclusion in the model resulted in a significant increase in the log-likelihood value from that of a reduced model, the random effect was retained. Heritabilities for each trait were estimated from these univariate analyses, while bivariate analyses provided estimates of phenotypic and genetic correlations among HCWT and the meat quality and nutritional value traits, fitting models to each trait based on the univariate analyses described above.

3. Results

3.1. Descriptive statistics

The unadjusted means and standard deviations for the meat quality and nutritional value traits are shown in Table 1. Considerable variability was evident for the fatty acids (range of

coefficient of variation (CV) from 31% to 53%), as well as the meat tenderness traits and indicators of muscle oxidative capacity (in this study, ICDH and Myo) which had CV greater than 25%. The mineral traits had moderate CV. The fresh meat colour and retail colour stability traits tended to be at least moderately variable. The least variable trait was pH₂₄LL with a coefficient of variation of 3%.

3.2. Heritability estimates

Estimates of variance components and derived genetic parameters are presented in Table 2. A high heritability value was obtained for IMF (0.48), whereas SF5 had a moderate heritability (0.27) and pH₂₄LL was lowly heritable (0.08). The indicators of muscle oxidative capacity and mineral traits were moderately heritable. Long chain omega-3 and omega-6 fatty acids tended to be of moderate heritability, apart from DPA and EPA+DPA+DHA which were of low heritability (estimates all less than 0.15). The meat colour traits tended to have moderate heritability estimates. Exceptions were the high heritability estimates obtained for *retL** and *reth* (estimates greater than 0.35) and the low heritability estimates obtained for *cfa**, *cfb** and *retb** (estimates about 0.10). HCWT was of moderate heritability (0.25). The sire x site interaction effect was significant for HCWT, SF5, *cfa**, *cfb** and *retL**, where it accounted for between 1.8% and 6.2% of the phenotypic variance in the meat quality traits. Among the meat quality traits, maternal genetic and environmental effects were important for *cfb**, *cfL**, IRON and the omega-6 fatty acids. The litter effect was important only for HCWT, LA and ARA.

3.3. Correlation estimates

3.3.1. Genetic correlations

3.3.1.1 HCWT and eating quality traits

Estimates of genetic correlations among HCWT and meat quality traits associated with meat tenderness, muscle oxidative capacity and mineral content are shown in Table 3. Genetic correlations between HCWT and IMF, SF5, ICDH, Myo and ZINC were all negligible and

not significantly different from zero based on their standard errors. Low negative genetic correlations were found between HCWT and pH₂₄LL (-0.32) and between HCWT and IRON (-0.28). For the meat tenderness traits, the strongest genetic correlations were found between IMF and SF5 (-0.62) and between pH₂₄LL and ZINC (0.46). Myo and IRON were very strongly correlated.

3.3.1.2 Fresh and retail meat colour

For the meat colour measures, strong positive genetic correlations were found for cfa^* and cfL^* with cfb^* (Table 4), but cfa^* and cfL^* were not genetically correlated. In contrast, the genetic correlation between $reta^*$ and $retb^*$ was moderate and positive while genetic correlations were moderate of $retL^*$ with $reta^*$ (-0.37) and $retb^*$ (0.36). The genetic correlations among $retOxy/Met$, $reth$ and $retC^*$ were high in magnitude (estimates greater than 0.7), with negative correlations involving $reth$ and a positive genetic correlation between $retOxy/Met$ and $retC^*$. Retail display meat a^* had very high genetic correlations with $retOxy/Met$, $reth$ and $retC^*$. Genetic correlations for $retL^*$ were moderate and negative with $retOxy/Met$, but strong and positive with $reth$.

Genetic correlations of the fresh meat colour measures with their corresponding retail colour stability measures were generally low, apart from a very high positive genetic correlation for the lightness measures (0.87). Fresh meat colour L^* was found to have a moderate positive genetic correlation with $reth$ and a moderate negative genetic correlation with $retOxy/Met$. A moderate negative genetic correlation was found between cfa^* and $reth$.

Myoglobin content had a moderate, positive genetic correlation with cfa^* (0.47) and strong, negative genetic correlations with cfL^* , $retL^*$, $retb^*$ and $reth$ (estimates all larger than -0.50). For ultimate pH, moderate, negative genetic correlations were found with $reta^*$ and $retOxy/Met$ while stronger, positive genetic correlations were found with $retL^*$ and $reth$.

3.3.1.3 Mineral and fatty acid traits

Estimates of genetic correlations among and between myoglobin concentration, the mineral traits and fatty acid traits are presented in Table 5. Genetic correlations among each of the individual long chain omega-3 and omega-6 fatty acids were positive, with the individual fatty acids being strongly correlated genetically with the sum EPA+DPA+DHA (range of 0.63 to 0.91). Although the genetic correlations between the long chain omega-3 and omega-6 fatty acids were generally positive, few significant correlations were found. Of the low, positive genetic correlations of fatty acids with myoglobin concentration and iron content, the correlations were significant for IRON with EPA and ARA. The fatty acids tended to be uncorrelated genetically with zinc content.

HCWT had generally very small genetic correlations with the meat colour traits and the fatty acids, with the estimates associated with relatively large standard errors (Table 6). Exceptions were the low positive genetic correlations between HCWT and *cfa** and *cfb**. While the genetic correlations between IMF and the fresh meat colour traits were positive (range of 0.26 to 0.81), those between SF5 and the fresh meat colour traits were negative (range of -0.19 to -0.61). Genetic correlations of IMF with *reta** and *retOxy/Met* were low and negative while a low, positive genetic correlation was found between IMF and *retL**. SF5 had moderate, positive genetic correlations with *reta** and *retOxy/Met*, but had low, negative genetic correlations with *retL** and *reth*. IMF had a strong, positive genetic correlation with LA (0.65). SF5 had small genetic correlations with the individual fatty acid traits, except for a moderate, negative genetic correlation with LA (-0.42). IMF had a moderate positive genetic correlation with LA+ARA, whereas SF5 had a small negative correlation.

Genetic and phenotypic correlation estimates of ICDH, the mineral traits and the fatty acids with the meat colour traits and of pH₂₄LL and ICDH with the fatty acids are provided as supplementary tables to this study (Tables S1 to S3). IRON had a strong positive genetic correlation with *cfa** (0.58) and strong, negative genetic correlations with *cfL** (-0.56), *retb** (-0.53), *retL** (-0.83) and *reth* (-0.51).

3.3.2. Phenotypic Correlations

Phenotypic correlation estimates among HCWT and the meat quality traits were generally smaller than 0.2 in magnitude and consistent with the direction of the corresponding genetic correlation (Tables 3, 4, 5 and 6). Stronger phenotypic correlation estimates were found for pairings of traits which had higher genetic correlations and were also usually smaller than the corresponding genetic correlation estimate. The stronger phenotypic correlations included: IMF and SF5 (-0.30); Myo and IRON (0.35); *cfb** with *cfa** (0.60) and *cfL** (0.40); and IMF and LA (0.38).

4. Discussion

The present study is among the first to present genetic and phenotypic correlation estimates across a wide range of objective measurements of meat quality and nutritional value traits of lamb, as well as heritability estimates for these traits. The recent study by Lorentzen & Vangen (2012), where the traits were recorded on 350 carcasses from a Norwegian breed, has also presented both correlation and heritability estimates for some quality traits of lamb meat. Earlier studies tended to report heritability estimates only for the meat quality traits, as reviewed by Hopkins et al. (2011), or correlation estimates among a limited number of meat quality traits such as ultimate pH and meat colour measures (Fogarty, Safari, Taylor & Murray, 2003; Ingham et al., 2007; Greef et al., 2008; Payne et al., 2009).

4.1 Heritability estimates

Overall, the meat quality traits in this study were found to be of moderate heritability and can be improved through selection. Improvement of several meat quality traits of Australian lamb appears to be warranted, as recent studies of meat samples from the Information Nucleus progeny have shown that at most 75% of the samples were considered tender after 5 days of ageing (Warner et al., 2010), 45% of the samples had intramuscular fat levels below 4% (Pannier et al., 2013b) and 49% of the samples were considered discoloured after 2 days of simulated retail display (Jacob et al., 2013), though 100% of the samples had acceptable meat redness (Warner et al., 2010). Studies with consumers of Australian lamb have shown

that acceptable eating quality requires low shear force values of less than 27 N and an intramuscular fat content of 5% (Hopkins, Hegarty, Walker & Pethick, 2006), while average acceptable levels of fresh meat redness are achieved above a threshold level of 9.5 (Khliji, van de Ven, Lamb, Lanza & Hopkins, 2010). Additionally, above a threshold level of 3.3 for oxy/met value, the ratio of reflectance of light in the wavelengths of 630 nm and 580 nm, Australian consumers have considered lamb meat to be of acceptable colour (red) while lamb meat with oxy/met values below 3.3 were considered discoloured (brown) (Khliji et al., 2010).

Heritability estimates for the meat quality traits related to meat palatability ranged from low to high. The high heritability estimate for IMF from this study was at the upper end of the range of published estimates (0.32 to 0.48) reported by Karamichou et al. (2006b), Mortimer et al. (2010) and Lorentzen & Vangen (2012). Shear force of the loin muscle as measured in this study was moderately heritable, with the estimate found to be at the lower end of the range of estimates (0.27 to 0.44) reviewed by Hopkins et al. (2011). Our estimates for both traits were very similar to estimates presented by Swan, Brown, Tier & van der Werf (2011), derived using both genomic and pedigree information and based on a sub-set of the data used in our study. The heritability estimate for ultimate pH was found to be low in this study and was less heritable than the estimates reviewed by Hopkins et al. (2011) and an estimate of 0.20 for ultimate pH recorded in the loin 48 hours after slaughter in a Norwegian terminal sire breed (Lorentzen & Vangen, 2012).

Among the fresh meat colour traits, the moderate heritability estimate for meat lightness (L^*) and the low heritability estimate for meat redness (a^*) found in our study were generally consistent with the reported values for these traits reviewed by Hopkins et al. (2011). Higher estimates have been reported for both lightness (estimates greater than 0.45; Cloete, Cloete, & Hoffman, 2008; Lorentzen & Vangen, 2012) and redness (estimates greater than 0.17; Karamichou et al., 2006b; Lorentzen & Vangen, 2012), but these estimates had large standard errors. Fresh meat yellowness (b^*) was found to be of low heritability and similar to estimates reported in Australian crossbred lamb and Merino populations (Ingham et al., 2007; Greef et

al., 2008). Much higher estimates (0.33, 0.29) were presented by Karamichou et al. (2006b) and Lorentzen & Vangen (2012) from studies using Scottish Blackface and Norwegian terminal sire lambs.

The generally moderate to high heritabilities estimated for many of the retail meat colour stability traits in the present study confirmed our previous findings that sufficient genetic variation in these traits exists to allow selection to reduce discolouration of lamb during retail display (Mortimer et al., 2010, Mortimer et al., 2011). For Australian lamb, Warner et al. (2007) had shown that loins from the Merino genotype generally were lighter, less red, more brown and had lower oxy/met values over 4 days of retail display than loins from Poll Dorset X Border Leicester Merino, Poll Dorset X Merino and Border Leicester X Merino genotypes. Improved stability of retail meat colour would extend the shelf life of lamb and have benefits for both consumers, who use meat colour as an indicator of lamb's freshness and quality, and for retailers for whom meat discolouration lowers the value of retail lamb cuts as a result of their shortened display life (Jacob et al., 2012). Heritability of meat colour stability traits under display conditions have only been previously reported for lightness, redness and yellowness of lamb loins (sampled from approximately 7,400 lambs from composite breed sires of the Poll Dorset, Suffolk and White Suffolk breeds) that were chilled for 8 weeks and displayed for 7 days (McLean, Johnson, Bain, Greer & Dodds, 2009) and lightness, redness, lightness and chroma of beef steaks aged 18 days and displayed for 6 days (King et al., 2010). Our heritability estimate for retail a^* value was very similar to the estimate (0.27 versus 0.26) of McLean et al. (2009). However, our heritability estimates for retail L^* were much higher (0.44 versus 0.23) and retail b^* much lower (0.04 versus 0.20) than estimates reported by those authors who displayed the meat in the dark as opposed to our study where samples were held under retail type lighting and measures were taken with a Hunter Miniscan. King et al. (2010) reported a high heritability estimate for retail lightness of beef steaks (0.40) and low estimates for redness and lightness (0.14, 0.13). Heritability of retail oxy/met value was high, with the only previous published estimates of moderate to high values being derived from sub-sets of the present study's data (Mortimer et al., 2010, 2011). Retail hue angle was found

to be of moderate heritability while retail chroma (or saturation index) was estimated to be of low heritability. Karamichou et al. (2006b) found hue angle of loin chops, recorded 24 hours post slaughter and after 2 hours of blooming, to be heritable (0.30), though these authors reported a high heritability estimate for chroma (0.45). Heritability estimates for hue angle and chroma have been reported also from studies of aged beef cuts from Piedmontese and Angus cattle, where Boukha et al. (2011) and Cecchinato, de Marchi, Penasa, Albera & Bittante (2011), using near-infrared spectroscopy predictions, presented estimates of 0.66 and 0.63 for hue angle and King et al. (2010), Boukha et al. (2011) and Cecchinato et al. (2011) presented estimates of 0.13, 0.16 and 0.15 for chroma.

The nutritional value traits were lowly to moderately heritable. While heritability of zinc content estimated in this study was very similar to the preliminary estimate reported by Mortimer et al. (2010), the heritability estimate for iron content reported here is almost double the estimate reported by the earlier study that used fewer records. Hermes & Jones (2012) have found iron content in pork LL to be highly heritable (0.34), where the mean iron content of the samples was 2.87 mg/kg and CV was 15%. A high heritability estimate (0.54) for iron content in beef steaks from Angus cattle has been reported by Mateescu et al. (2013). For zinc content in beef steaks, these authors reported a low heritability estimate (0.09), which was lower than the present study's estimate.

Heritability estimates for the long chain omega-3 and omega-6 fatty acids were generally moderate. Heritability estimates for EPA and DHA were at the lower and mid points of the ranges of estimates for these fatty acids in sheep meat (0.18 to 0.29 for EPA and 0.16 to 0.25 for DHA) reviewed by Hopkins et al. (2011). The heritability estimate for DPA reported in this study was much lower than estimates of 0.13 and 0.24 presented by Karamichou, Richardson, Nute, Gibson, & Bishop (2006a) in Scottish Blackface sheep and Greeff, Harvey, Young, Kitessa, & Dowling (2007) in Australian Merino sheep. These authors have also reported heritability estimates for LA and ARA. In contrast to the moderate estimate from the present study, LA was found to be of low heritability (0.10) by Karamichou et al. (2006a). As well, both Karamichou et al. (2006a) and Greeff et al. (2007) reported much higher

heritability estimates for ARA (0.60, 0.35) than our estimate. For lamb produced under a range of production environments across Australia, only in about 25% of slaughter groups have health-claimable levels (exceeding 23mg/100g meat) of the long chain omega-3 fatty acids, sum of EPA and DHA, been recorded in loin samples from 95% of the lambs within a slaughter group (Ponnampalam et al., 2013). Though the present study has found that long-chain omega-3 fatty acids can be improved by selection, their levels have been shown to be more sensitive to the diet consumed by the lambs (Ponnampalam et al., 2012) and that achieving high levels of these health-claimable fatty acids is best done by providing lambs with an appropriate finishing diet (Ponnampalam et al., 2013).

The indicators of the oxidative capacity of muscle, ICDH and Myo, were both moderately heritable. The ICDH activity of the loin, but not its myoglobin content, has previously been shown to differ between genotypes representative of those used in the Australian lamb industry (Gardner et al., 2007). The activity of ICDH was also found to be moderately heritable (0.28) in LL muscle collected from a very small sample of Limousin bulls (Renand et al., 1995). For other muscle enzyme activities, heritability estimates of 0.31 and 0.44 for lactate dehydrogenase activity of LL muscle in Limousin bulls (Renand et al., 1995) and Large White pigs (Larzul et al., 1999) and 0.22 for citrate synthase activity in Large White pigs (Larzul et al., 1999) have been reported. Heritability of myoglobin content estimated in the present study was little different to the earlier estimate from the same data source presented by Mortimer et al. (2010) and consistent with a previous estimate of 0.27 for soluble myoglobin content in pork LL (Newcom et al., 2004).

The moderate heritability for HCWT presented in this study was lower than the earlier estimate based on a sub-set of the present data (0.27 versus 0.35) and estimates reported by Ingham et al. (2007) and Greeff et al. (2008), but higher than a mean estimate of 0.20 presented by Safari, Fogarty & Gilmour (2005).

4.2. Correlation estimates

Selection for increased HCWT is expected to yield minimal changes in the meat quality traits, as HCWT and most meat quality traits were found to be very weakly genetically correlated in this study. One exception was the low, negative genetic correlation of HCWT with ultimate pH, which was stronger than estimates of -0.22 reported by Ingham et al. (2007) and 0.03 reported by Payne et al. (2009), such that increasing HCWT through selection would reduce the ultimate pH. With respect to iron, increasing HCWT would lead also to a small reduction in the iron content of lamb meat. This relationship is in contrast to the small, favourable genetic correlation between average daily gain and iron content in pork reported by Hermesch & Jones (2012), though both estimates were associated with relatively large standard errors. In the most recent study of iron content of Australian lamb loins, the muscle iron content was found to exceed 2 mg/100 g in only 48% of muscle samples from Information Nucleus lambs, a content which can be claimed as a 'good source' for men of all ages and for women more than 50 years old (Pannier et al., 2013a). To maintain or improve lamb meat's ability to meet recommended dietary intakes of iron, monitoring should be undertaken of the iron content of lamb meat produced from breeding programmes that emphasise carcass weight to identify if selection emphasis should be directed towards changing lamb's iron content.

From our study, small increases in fresh meat redness and yellowness are expected also from selection for HCWT. Ingham et al. (2007) earlier found a low, positive genetic correlation between HCWT and fresh meat lightness (0.34 ± 0.21) whereas Payne et al. (2009) reported a weak, negative genetic correlation between these traits that was not significantly different from zero. Payne et al. (2009) also reported a low, negative genetic correlation (-0.29) between carcass weight and fresh meat redness. McLean et al. (2009) reported genetic correlations of HCWT with retail display

redness (0.13), lightness (-0.30) and yellowness (-0.25) that were consistent in direction to estimates for comparable trait combinations from the present study.

Higher levels of intramuscular fat were associated genetically with lower shear force values (more tender meat), a finding consistent with the strong negative genetic correlation between IMF and shear force reported by Karamichou et al. (2006b) in Scottish Blackface sheep. Consistent with this genetic correlation, the genetic relationships of IMF and shear force with the fresh meat colour traits were positive and negative respectively. Selection to increase IMF or reduce shear force values would increase the fresh meat measures of b^* value (meat more yellow in colour) and L^* value (lighter or paler meat), as well as a^* value (redder meat) to a lesser extent. Lorentzen & Vangen (2012) had reported negative genetic correlation estimates, though not significantly different from zero, between IMF and a^* , b^* and L^* values. Similar to our results, Wolcott et al. (2009) have reported a positive genetic correlation (0.45) between IMF and L^* value and negative genetic correlations between shear force measures and L^* values (-0.41, -0.22) in beef. Similar consistency among the genetic correlations of IMF and SF5 with each of the retail colour traits was also observed. However, some unfavourable genetic correlations were found with IMF and SF5 (retail oxy/met, redness and hue angle values), which indicate that selection for more desirable levels of IMF (higher values) and SF5 (lower values) would be associated with lamb meat becoming discoloured slightly more rapidly and less red in colour during retail display. The favourable genetic correlations of IMF and SF5 with retail L^* value suggests that such selection would also be associated with lighter meat colour during retail display. McLean et al. (2009) reported a significant negative genetic correlation between tenderness and L^* value (-0.20) of lamb measured after 8 weeks chilled storage and 7 days after cutting,

although genetic correlations of tenderness with a^* and b^* values were not significantly different from zero.

Selection for redder meat will increase yellowness only of fresh lamb meat, as fresh meat a^* and L^* with b^* genetic correlations were strong and positive while fresh meat a^* and L^* were uncorrelated genetically. Greeff et al. (2008) reported similar genetic correlation estimates of a^* and L^* with b^* in Merino sheep, though found a^* and L^* to have a moderate, positive genetic correlation. a^* and L^* were found to be uncorrelated genetically in a multi-breed flock (Payne et al., 2009). A strong positive genetic correlation between L^* and b^* has also been reported by Lorentzen & Vangen (2012), but these authors found a^* and b^* to be uncorrelated genetically and a^* and L^* to have a strong negative genetic correlation. Correlation estimates among colour stability measures have only been derived and presented by McLean et al. (2009) and from a sub-set of the present study's data by Mortimer et al. (2010, 2011). Whereas McLean et al. (2009) reported significant positive genetic correlations only of L^* with a^* (0.12) and b^* (0.60), the correlations estimated by the present study were positive and favourable for b^* with a^* and L^* and negative and unfavourable for a^* with L^* . The very strong and favourable genetic correlations among a^* , hue and oxy/met values during retail display (all greater than 0.9) indicate that these traits are being influenced by very similar sets of genes. Selection for higher retail a^* value is expected to result in substantial correlated responses, such that lamb meat will be less brown (higher oxy/met value) and more red (lower hue) during retail display.

Estimates of genetic correlations between the fresh meat colour traits and ultimate pH were generally weak and tended to be negative, indicating that reducing pH genetically is expected to lead to only marginal changes in a^* and b^* values. These estimates agreed with those reported for relationships involving a^* and L^* by some

authors in crossbred progeny of maternal sire breeds (Ingham et al., 2007) and terminal sire breeds (Payne et al. 2009), but not with strong, negative estimates involving a^* , b^* and L^* reported in Merino sheep (Fogarty et al., 2003; Greeff et al., 2008). Processing conditions (e.g. ageing protocols, electrical stimulation) may explain these differences between the studies and also important is the propensity for Merino lambs to achieve much higher pH levels (Hopkins & Fogarty, 1998). In contrast, the relationships of pH with the retail colour traits indicate that reducing pH genetically would result in increases in a^* (redder meat), oxy/met (less brown meat) and hue values (less discoloured meat) and a decrease in L^* (darker meat). These genetic relationships are not consistent with those reported by McLean et al. (2009) who found that pH had significant negative genetic correlations with a^* and L^* only.

The almost unity genetic correlation between iron and myoglobin contents indicates that these traits are genetically the same. In accordance with this, genetic correlation estimates for these two traits with each of the remaining meat quality traits were very similar. Increasing iron content through selection is expected to lead to fresh meat colour being redder, but darker due to changes in a^* and L^* , while meat colour during retail display is expected to be less yellow, darker and less discoloured due to changes in b^* , L^* and hue values under simulated retail conditions. In reasonable agreement with our results, Hermesch & Jones (2012) have reported genetic correlation estimates for iron content in pork loin that are positive with fresh meat a^* (0.94) and b^* (0.50) values and negative with L^* (-0.59) values. These authors also reported a low, negative genetic correlation between iron content and pH (-0.24) which agreed with our estimate for this genetic correlation (-0.29).

5. Conclusions

The national genetic evaluation programme for the Australian sheep industry, Sheep Genetics (Brown et al., 2006), has developed research breeding values for hot carcass weight, intramuscular fat and shear force for terminal sires that have participated in the Information Nucleus programme (see <http://www.sheepgenetics.org.au/Resources/Genomic-Results>). For these traits, this study has confirmed the extent of genetic variation in the traits that is available to be exploited through sheep breeding programmes. The moderate heritability estimates for many of the meat quality traits have indicated that there is sufficient genetic variation in most fresh meat colour, retail colour stability and nutritional value traits to allow these quality attributes of lamb to be changed through selection. With the genetic relationships between hot carcass weight and the meat quality traits being generally favourable and small, breeding programmes that have a selection emphasis on hot carcass weight are expected to yield few substantial, deleterious changes in those traits. However, the relationship between hot carcass weight and iron content is unfavourable and both traits would need to be considered in breeding programmes in order to avoid unfavourable changes in the iron levels of lamb. Additionally, the likely genetic responses in other meat quality traits will need to be evaluated when developing selection strategies aimed at increasing intramuscular fat levels in lamb or improving its tenderness. For these selection strategies, the genetic parameters for both intramuscular fat and shear force indicate that while favourable responses in fresh meat colour measures and most other meat quality traits are expected, unfavourable changes in the colour stability of lamb during retail display are predicted to occur to a lesser extent.

A more detailed understanding of the potential role of meat quality traits in breeding objectives and as selection criteria for sheep meat breeding programmes also

requires estimates of the correlations, genetic and phenotypic, of meat quality traits with growth and assessments of muscle and fat levels in live animals and carcasses. From the estimates available from this study and those of Mortimer et al. (2010), fresh meat redness, due to its strong positive genetic correlation with ultrasound fat depth, and retail meat redness and oxy/met values appear to be potential traits for inclusion in sheep meat breeding objectives. As has been investigated in pork (Hermesch & Jones, 2012), fresh meat redness may also prove to be a useful selection criteria for the improvement of iron content of lamb. Genetic analyses of the complete data on growth, carcass composition and meat quality traits recorded on progeny and carcasses produced by the Information Nucleus programme and modelling of a range of selection strategies to improve lamb production and its quality will verify if this should occur for these and other meat quality traits.

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Table 1

Descriptive unadjusted statistics for hot carcass weight and meat quality and nutritional value traits.

Trait ^a	n	Mean	SD	Minimum	Maximum	CV
HCWT (kg)	8968	23.1	3.8	12.5	40.0	16.3
Meat quality traits						
IMF (%)	5735	4.23	1.05	1.50	10.45	24.8
SF5 (N)	5572	26.9	9.7	10.8	95.1	36.2
pH ₂₄ LL	7805	5.66	0.14	5.21	6.87	2.5
ICDH (μmol/min/g tissue)	3248	5.14	1.67	1.02	11.40	32.4
Myo (mg/g tissue)	5727	6.63	1.84	2.16	15.62	27.7
cfa*	7200	18.6	2.4	9.8	30.0	12.7
cfb*	7201	3.8	4.2	-5.4	19.4	113.0
cfL*	7198	34.7	3.1	24.4	46.0	8.8
reta*	4459	16.5	2.5	9.6	27.7	15.1
retb*	4455	17.5	2.5	8.7	26.6	14.2
retL*	4459	36.6	2.9	26.8	47.8	7.8
retOxy/Met	4459	3.5	0.9	1.9	9.9	25.0
reth	4455	46.7	3.1	30.5	58.6	6.9
retC*	4458	24.1	3.3	13.9	38.3	13.6
Nutritional value traits						
IRON (mg/kg wet tissue)	5716	20.29	3.66	8.12	45.11	18.0
ZINC (mg/kg wet tissue)	5716	24.30	4.40	11.81	44.88	18.1
EPA (mg/ 100g tissue)	5722	15.74	8.33	1.51	54.97	52.9
DPA (mg/ 100g tissue)	5724	24.33	8.68	5.06	71.06	35.7
DHA (mg/ 100g tissue)	5718	7.18	3.02	0.04	23.56	42.1
EPA+DHA (mg/ 100g tissue)	5716	22.92	10.83	2.61	69.35	47.3
EPA+DPA+DHA (mg/ 100g tissue)	5716	47.26	18.33	8.83	122.30	38.8
LA (mg/ 100g tissue)	5716	131.90	42.49	51.84	337.10	32.2
ARA (mg/ 100g tissue)	5719	44.53	14.89	15.15	110.40	33.4
LA+ARA (mg/ 100g tissue)	5715	176.40	54.87	71.64	436.00	31.1

^a HCWT = hot carcass weight; IMF = intramuscular fat; SF5 = shear force measured after 5 days ageing; pH₂₄LL = pH at 24 h after slaughter; ICDH = isocitrate dehydrogenase activity; Myo = myoglobin concentration; cfa* = fresh meat redness; cfb* = fresh meat yellowness; cfL* = fresh meat lightness; reta* = retail display meat redness; retb* = retail display meat yellowness; retL* = retail display meat lightness; retOxy/Met = retail display meat oxy/met value; reth = retail display meat hue [$h = \tan^{-1}(b^*/a^*)$]; retC* = retail display meat chroma [$C^* = (a^{*2} + b^{*2})^{0.5}$]; IRON = iron content of wet muscle tissue; ZINC = zinc content of wet muscle tissue; EPA = eicosapentaenoic acid content of wet muscle tissue; DPA = docosapentaenoic acid content of wet muscle tissue; DHA = docosahexaenoic acid content of wet muscle tissue; EPA+DHA = sum of EPA and DHA; EPA+DPA+DHA = sum of EPA, DPA and DHA; LA = linoleic acid content of wet muscle tissue; ARA = arachidonic acid content of wet muscle tissue; LA+ARA = sum of LA and ARA.

Table 2

Estimates (standard errors) of phenotypic (σ^2_P), additive genetic (σ^2_A) and sire x site interaction ($\sigma^2_{\text{Sire X Site}}$) variances, heritability (h^2), maternal environmental variance (c^2) and litter variance (l^2) for the meat traits measured on lamb carcasses.

Trait ^a	σ^2_P	σ^2_A	$\sigma^2_{\text{Sire X Site}}$	h^2	c^2	l^2
HCWT	5.41	1.44	0.33	0.25 (0.04)	0.03 (0.02)	0.08 (0.03)
Meat quality traits						
IMF	0.679	0.326		0.48 (0.05)		
SF5	51.24	14.07	1.39	0.27 (0.04)		
pH ₂₄ LL	0.009	0.001		0.08 (0.02)		
ICDH	0.977	0.195		0.20 (0.04)		
Myo	1.421	0.350		0.25 (0.03)		
cfa*	1.83	0.14	0.05	0.08 (0.03)		
cfb*	1.24	0.13	0.02	0.10 (0.03)	0.05 (0.02)	
cfL*	3.99	0.72		0.18 (0.03)	0.04 (0.02)	
reta*	2.72	0.68		0.25 (0.04)		
retb*	1.85	0.19		0.10 (0.03)		
retL*	4.23	1.73	0.09	0.41 (0.05)		
retOxy/Met	0.37	0.10		0.27 (0.04)		
reth	4.78	1.73		0.36 (0.05)		
retC*	3.76	0.60		0.16 (0.04)		
Nutritional value traits						
IRON	8.31	1.76		0.21 (0.04)	0.04 (0.02)	
ZINC	15.15	4.04		0.27 (0.04)		
EPA ^b	0.066	0.011		0.17 (0.03)		
DPA	0.047	0.002		0.05 (0.02)		
DHA	0.088	0.020		0.22 (0.03)		
EPA+DHA	0.058	0.009		0.16 (0.03)		
EPA+DPA+DHA	0.044	0.004		0.08 (0.02)		
LA	0.025	0.005		0.22 (0.04)	0.02 (0.03)	0.10 (0.04)
ARA	0.025	0.004		0.15 (0.04)	0.02 (0.03)	0.08 (0.04)
LA+ARA	0.021	0.004		0.20 (0.04)		

^aSee Table 1 for trait abbreviations.

^bData for the fatty acids (EPA, DPA, DHA, EPA+DHA, EPA+DPA+DHA, LA, ARA and LA+ARA) were log transformed before estimation of variances and variance ratios.

Table 3

Genetic and phenotypic correlation estimates^a (standard errors) among hot carcass weight and meat quality traits.

	HCWT	IMF	SF5	pH ₂₄ LL	ICDH	Myo	IRON	ZINC
HCWT ^b		0.15	-0.14	-0.12	0.00	0.10	0.04	0.02
IMF	0.06 (0.08)		-0.30	-0.07	0.08	0.05	0.05	0.04
SF5	-0.06 (0.10)	-0.62 (0.07)		0.09	-0.12	-0.10	-0.07	-0.02
pH ₂₄ LL	-0.32 (0.12)	0.03 (0.14)	-0.21 (0.16)		-0.05	-0.01	-0.06	0.06
ICDH	-0.02 (0.13)	0.03 (0.13)	-0.27 (0.14)	-0.10 (0.22)		0.14	0.21	0.12
Myo	0.08 (0.10)	-0.05 (0.09)	-0.08 (0.10)	-0.11 (0.16)	0.41 (0.13)		0.35	0.09
IRON	-0.28 (0.11)	0.02 (0.10)	-0.04 (0.11)	-0.31 (0.16)	0.49 (0.12)	0.97 (0.05)		0.18
ZINC	-0.05 (0.10)	0.09 (0.09)	-0.04 (0.10)	0.46 (0.14)	0.22 (0.14)	0.21 (0.10)	0.17 (0.11)	

^a Estimates of genetic correlations (below diagonal) and phenotypic correlations (above diagonal and with standard errors all less than 0.02) .

^b See Table 1 for trait abbreviations.

Table 4

Genetic and phenotypic correlation estimates^a (standard errors) among fresh and retail meat colour traits, ultimate pH and myoglobin concentration.

	<i>cfa</i> *	<i>cfb</i> *	<i>cfL</i> *	<i>reta</i> *	<i>retb</i> *	<i>retL</i> *	<i>retOxy/Met</i>	<i>reth</i>	<i>retC</i> *	pH ₂₄ LL	Myo
<i>cfa</i> * ^b		0.60	0.00	0.16	0.05	-0.09	0.09	-0.22	0.12	-0.22	0.12
<i>cfb</i> *	0.61 (0.10)		0.40	0.19	0.17	0.19	0.12	-0.09	0.19	-0.24	-0.01
<i>cfL</i> *	-0.08 (0.14)	0.57 (0.11)		0.06	0.20	0.42	0.00	0.14	0.14	-0.14	-0.21
<i>reta</i> *	0.30 (0.14)	-0.08 (0.14)	-0.35 (0.12)		0.67	-0.27	0.95	-0.51	0.89	-0.20	0.07
<i>retb</i> *	0.21 (0.20)	-0.08 (0.20)	0.18 (0.17)	0.48 (0.12)		0.05	0.60	0.20	0.90	-0.02	-0.07
<i>retL</i> *	-0.19 (0.12)	0.29 (0.11)	0.87 (0.06)	-0.37 (0.09)	0.36 (0.13)		-0.35	0.41	-0.11	0.07	-0.37
<i>retOxy/Met</i>	0.20 (0.14)	-0.17 (0.14)	-0.40 (0.11)	0.98 (0.01)	0.43 (0.13)	-0.45 (0.08)		-0.52	0.83	-0.17	0.06
<i>reth</i>	-0.32 (0.14)	0.03 (0.14)	0.51 (0.12)	-0.91 (0.06)	-0.18 (0.19)	0.62 (0.08)	-0.90 (0.06)		-0.17	0.21	-0.13
<i>retC</i> *	0.24 (0.16)	-0.15 (0.16)	-0.13 (0.14)	0.83 (0.04)	0.79 (0.06)	-0.02 (0.11)	0.80 (0.05)	-0.72 (0.12)		-0.12	-0.02
pH ₂₄ LL	-0.29 (0.17)	-0.12 (0.17)	0.06 (0.15)	-0.42 (0.15)	0.00 (0.23)	0.54 (0.12)	-0.42 (0.14)	0.62 (0.14)	-0.19 (0.18)		-0.01
Myo	0.47 (0.13)	-0.08 (0.14)	-0.81 (0.08)	0.20 (0.12)	-0.57 (0.17)	-0.83 (0.06)	0.24 (0.12)	-0.52 (0.12)	-0.17 (0.14)	-0.11 (0.16)	

^a Estimates of genetic correlations (below diagonal) and phenotypic correlations (above diagonal and with standard errors all less than 0.02) .

^b See Table 1 for trait abbreviations.

Table 5

Genetic and phenotypic correlation estimates^a (standard errors) among myoglobin concentration, mineral and fatty acid traits.

	Myo	IRON	ZINC	EPA	DPA	DHA	EPA+DHA	EPA+DPA+DH A	LA	ARA	LA+ARA
Myo ^b		0.35	0.09	-0.01	0.00	0.03	0.01	0.01	0.04	0.04	0.04
IRON	0.97 (0.05)		0.18	0.06	0.04	0.09	0.08	0.07	0.11	0.11	0.12
ZINC	0.21 (0.10)	0.17 (0.11)		-0.07	-0.03	-0.03	-0.06	-0.05	0.03	0.00	0.02
EPA	0.20 (0.12)	0.29 (0.13)	-0.11 (0.12)		0.69	0.58	0.94	0.88	0.26	0.40	0.34
DPA	0.17 (0.19)	0.36 (0.19)	-0.04 (0.19)	0.69 (0.12)		0.57	0.72	0.93	0.36	0.47	0.44
DHA	0.09 (0.11)	0.20 (0.11)	-0.09 (0.11)	0.35 (0.11)	0.23 (0.18)		0.81	0.74	0.28	0.40	0.35
EPA+DHA	0.19 (0.12)	0.29 (0.13)	-0.15 (0.12)	0.90 (0.02)	0.63 (0.13)	0.69 (0.06)		0.92	0.31	0.45	0.39
EPA+DPA+DH A	0.20 (0.15)	0.37 (0.15)	-0.14 (0.15)	0.91 (0.03)	0.82 (0.07)	0.61 (0.10)	0.96 (0.02)		0.36	0.50	0.45
LA	0.02 (0.11)	0.12 (0.13)	0.06 (0.11)	-0.01 (0.13)	0.37 (0.18)	0.24 (0.11)	0.15 (0.13)	0.26 (0.15)		0.50	0.97
ARA	0.22 (0.12)	0.35 (0.13)	0.04 (0.12)	0.17 (0.14)	0.18 (0.21)	0.42 (0.11)	0.35 (0.13)	0.29 (0.16)	0.28 (0.13)		0.69
LA+ARA	0.06 (0.12)	0.23 (0.12)	0.06 (0.12)	0.01 (0.13)	0.34 (0.18)	0.28 (0.11)	0.19 (0.13)	0.27 (0.15)	0.97 (0.01)	0.49 (0.10)	

^a Estimates of genetic correlations (below diagonal) and phenotypic correlations (above diagonal and with standard errors all less than 0.02) .

^b See Table 1 for trait abbreviations.

Table 6

Genetic and phenotypic correlation estimates (standard errors^a) for hot carcass weight, intramuscular fat and shear force with meat colour and fatty acid traits.

	Genetic correlation			Phenotypic correlation		
	HCWT	IMF	SF5	HCWT	IMF	SF5
<i>cf_a</i> ^b	0.23 (0.11)	0.26 (0.12)	-0.19 (0.14)	0.13	0.14	-0.16
<i>cf_b</i> [*]	0.19 (0.12)	0.81 (0.08)	-0.61 (0.12)	0.14	0.25	-0.19
<i>cf_L</i> [*]	0.25 (0.11)	0.56 (0.09)	-0.38 (0.11)	0.03	0.21	-0.11
<i>ret_a</i> [*]	0.13 (0.10)	-0.21 (0.11)	0.33 (0.12)	0.22	-0.06	0.02
<i>ret_b</i> [*]	-0.07 (0.15)	-0.06 (0.16)	0.05 (0.17)	0.10	0.02	-0.03
<i>ret_L</i> [*]	-0.09 (0.08)	0.35 (0.08)	-0.27 (0.10)	-0.12	0.20	-0.04
<i>retOxy/Met</i>	0.16 (0.10)	-0.27 (0.10)	0.43 (0.11)	0.21	-0.12	0.05
<i>reth</i>	-0.16 (0.10)	0.17 (0.11)	-0.35 (0.12)	-0.18	0.09	-0.06
<i>retC</i> [*]	-0.13 (0.12)	(0.12)	0.30 (0.14)	0.17	-0.03	-0.01
EPA	-0.03 (0.12)	-0.15 (0.11)	0.16 (0.12)	-0.08	-0.06	0.02
DPA	-0.18 (0.18)	0.14 (0.17)	(0.19)	-0.02	0.06	-0.02
DHA	-0.01 (0.10)	(0.10)	0.20 (0.11)	0.00	0.02	0.00
EPA+DHA	-0.09 (0.12)	(0.11)	0.20 (0.12)	-0.06	-0.03	0.01
EPA+DPA+DHA	0.02 (0.12)	0.01 (0.14)	0.02 (0.15)	-0.04	0.02	-0.01
LA	-0.42 (0.12)	0.65 (0.07)	(0.10)	0.12	0.38	-0.17
ARA	-0.07 (0.13)	-0.22 (0.10)	0.09 (0.12)	-0.03	-0.05	0.03
LA+ARA	-0.32 (0.11)	0.50 (0.08)	(0.11)	0.09	0.30	-0.13

^a Standard errors all less than 0.02 for the phenotypic correlations.

^b See Table 1 for trait abbreviations.

Supplementary tables

Table S1Genetic correlation estimates (standard errors) for fresh and retail meat colour traits with ICDH activity, mineral and fatty acid traits^a.

	<i>cfa</i> *	<i>cfb</i> *	<i>cfL</i> *	<i>reta</i> *	<i>retb</i> *	<i>retL</i> *	<i>retOxy/Met</i>	<i>reth</i>	<i>retC</i> *
ICDH	0.15 (0.20)	0.02 (0.19)	-0.16 (0.17)	-0.34 (0.16)	-0.24 (0.23)	-0.30 (0.13)	-0.37 (0.15)	0.28 (0.16)	-0.40 (0.17)
IRON	0.58 (0.13)	0.18 (0.16)	-0.56 (0.12)	0.17 (0.13)	-0.53 (0.18)	-0.83 (0.06)	0.20 (0.13)	-0.51 (0.12)	-0.13 (0.14)
ZINC	0.24 (0.14)	0.03 (0.14)	0.01 (0.12)	-0.14 (0.12)	-0.26 (0.18)	0.02 (0.10)	-0.14 (0.12)	0.10 (0.12)	-0.18 (0.14)
EPA	0.06 (0.17)	-0.08 (0.17)	-0.16 (0.15)	0.05 (0.15)	0.01 (0.20)	-0.29 (0.12)	0.12 (0.14)	0.05 (0.15)	0.04 (0.17)
DPA	0.01 (0.25)	0.02 (0.25)	0.04 (0.22)	0.17 (0.22)	0.10 (0.30)	-0.33 (0.19)	0.22 (0.21)	-0.07 (0.22)	0.13 (0.24)
DHA	0.09 (0.15)	0.04 (0.15)	0.03 (0.13)	-0.06 (0.13)	-0.19 (0.18)	-0.19 (0.11)	-0.05 (0.12)	-0.07 (0.13)	-0.14 (0.14)
EPA+DHA	0.08 (0.17)	-0.01 (0.17)	-0.06 (0.15)	0.03 (0.15)	-0.01 (0.20)	-0.29 (0.12)	0.07 (0.14)	0.00 (0.15)	-0.01 (0.17)
EPA+DPA+DHA	0.10 (0.21)	0.03 (0.20)	0.01 (0.18)	0.09 (0.18)	-0.01 (0.25)	-0.34 (0.15)	0.13 (0.17)	-0.04 (0.18)	0.05 (0.20)
LA	0.20 (0.16)	0.54 (0.15)	0.53 (0.12)	-0.37 (0.13)	-0.21 (0.19)	0.11 (0.11)	-0.45 (0.12)	0.28 (0.13)	-0.38 (0.15)
ARA	0.26 (0.17)	-0.05 (0.18)	-0.08 (0.16)	-0.13 (0.15)	-0.09 (0.21)	-0.25 (0.12)	-0.10 (0.14)	0.15 (0.15)	-0.30 (0.16)
LA+ARA	0.24 (0.16)	0.43 (0.14)	0.42 (0.12)	-0.34 (0.13)	-0.24 (0.20)	0.01 (0.12)	-0.39 (0.12)	0.27 (0.14)	-0.39 (0.15)

^a ICDH = isocitrate dehydrogenase activity; *cfa** = fresh meat redness; *cfb** = fresh meat yellowness; *cfL** = fresh meat lightness; ; *reta** = retail display meat redness; *retb**= retail display meat yellowness; *retL** = retail display meat lightness; *retOxy/Met* = retail display meat oxy/met value; *reth* = retail display meat hue [$h = \tan^{-1}(b^*/a^*)$]; *retC**= retail display meat chroma [$C^* = (a^{*2} + b^{*2})^{0.5}$]; IRON = iron content of wet muscle tissue; ZINC = zinc content of wet muscle tissue; EPA = eicosapentaeonic acid content of

wet muscle tissue; DPA = docosapentaeonic acid content of wet muscle tissue; DHA = docosahexaeonic acid content of wet muscle tissue; EPA+DHA = sum of EPA and

DHA; EPA+DPA+DHA = sum of EPA, DPA and DHA; LA = linoleic acid content of wet muscle tissue; ARA = arachidonic acid content of wet muscle tissue; LA+ARA =

sum of LA and ARA.

Table S2

Phenotypic correlation estimates (standard errors all less than 0.02) for fresh and retail meat colour traits with ICDH activity, mineral and fatty acid traits^a.

	<i>cfa</i> *	<i>cfb</i> *	<i>cfL</i> *	<i>reta</i> *	<i>retb</i> *	<i>retL</i> *	<i>retOxy/Met</i>	<i>reth</i>	<i>retC</i> *
ICDH	0.10	-0.04	-0.16	-0.13	-0.08	-0.13	-0.12	0.08	-0.11
IRON	0.12	-0.04	-0.25	0.00	-0.10	-0.39	-0.01	-0.12	-0.06
ZINC	0.03	0.03	-0.01	-0.01	0.00	-0.01	-0.01	0.01	-0.02
EPA	-0.03	-0.04	-0.09	-0.04	-0.02	-0.07	-0.03	0.03	-0.03
DPA	-0.01	0.00	-0.03	-0.03	-0.01	-0.02	-0.04	0.03	-0.02
DHA	-0.01	-0.01	-0.07	-0.02	-0.02	-0.08	-0.02	0.02	-0.02
EPA+DHA	-0.02	-0.04	-0.09	-0.03	-0.02	-0.08	-0.03	0.03	-0.03
EPA+DPA+DHA	-0.02	-0.02	-0.06	-0.04	-0.02	-0.05	-0.04	0.04	-0.03
LA	0.06	0.06	0.03	-0.11	-0.06	-0.05	-0.16	0.04	-0.09
ARA	0.01	-0.04	-0.07	-0.09	-0.07	-0.09	-0.10	0.02	-0.10
LA+ARA	0.06	0.05	0.01	-0.12	-0.07	0.00	-0.16	0.04	-0.10

^a ICDH = isocitrate dehydrogenase activity; *cfa** = fresh meat redness; *cfb** = fresh meat yellowness; *cfL** = fresh meat lightness; ; *reta** = retail display meat redness; *retb** = retail display meat yellowness; *retL** = retail display meat lightness; *retOxy/Met* = retail display meat oxy/met value; *reth* = retail display meat hue [$h = \tan^{-1}(b^*/a^*)$]; *retC** = retail display meat chroma [$C^* = (a^{*2} + b^{*2})^{0.5}$]; IRON = iron content of wet muscle tissue; ZINC = zinc content of wet muscle tissue; EPA = eicosapentaeonic acid content of wet muscle tissue; DPA = docosapentaeonic acid content of wet muscle tissue; DHA = docosahexaeonic acid content of wet muscle tissue; EPA+DHA = sum of EPA and DHA; EPA+DPA+DHA = sum of EPA, DPA and DHA; LA = linoleic acid content of wet muscle tissue; ARA = arachidonic acid content of wet muscle tissue; LA+ARA = sum of LA and ARA.

Table S3

Genetic and phenotypic correlation estimates (standard errors) for pH₂₄LL and ICDH with fatty acid traits^a.

	Genetic correlations		Phenotypic correlations	
	pH ₂₄ LL	ICDH	pH ₂₄ LL	ICDH
EPA	-0.43 (0.18)	0.09 (0.17)	-0.02	0.08
DPA	-0.26 (0.28)	0.28 (0.24)	-0.01	0.08
DHA	-0.27 (0.16)	0.05 (0.15)	-0.03	0.06
EPADHA	-0.50 (0.18)	0.07 (0.17)	-0.03	0.11
EPADPADHA	-0.47 (0.23)	0.17 (0.20)	-0.02	0.11
LA	-0.19 (0.17)	0.24 (0.14)	-0.06	0.19
ARA	-0.27 (0.20)	0.29 (0.16)	-0.02	0.15
LAARA	-0.24 (0.18)	0.23 (0.15)	-0.05	0.20

^a pH₂₄LL = pH at 24 h after slaughter; ICDH = isocitrate dehydrogenase activity; EPA = eicosapentaeonic acid content of wet muscle tissue; DPA = docosapentaeonic acid content of wet muscle tissue; DHA = docosahexaeonic acid content of wet muscle tissue; EPADHA = sum of EPA + DHA; EPADPADHA = sum of EPA + DPA + DHA; LA = linoleic acid content of wet muscle tissue; ARA = arachidonic acid content of wet muscle tissue; LAARA = sum of LA + ARA.

Highlights

- Genetic parameters were estimated among a range of meat quality traits in lamb meat.
- Moderate heritability of many traits showed that they can be altered via selection.
- Selection to improve IMF or tenderness associated with reduced meat colour stability.
- Meat redness and iron content could possibly be included in sheep breeding programmes.